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Permanent Tooth Calcification in Chimpanzees (*Pan troglodytes*): Patterns and Polymorphisms

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ABSTRACT Tooth calcification is an important developmental marker for use in constructing models for early hominid life history, particularly for its application to the fossil record. As chimpanzees are commonly utilized in interspecific comparisons in such research, this study aims to improve available baseline data for tooth calcification patterns in chimpanzees (*Pan troglodytes*), and to quantify basic patterns and polymorphisms. We present an analysis of developmental patterns for the left mandibular dentition (I_1–M_3) based on intraoral radiographs obtained from a cross-sectional sample of chimpanzees (58 males, 60 females) housed at LEMSIP (NYU Medical Center) and Yerkes (Emory University). No significant differences with previous descriptions of the basic sequences of tooth calcification in chimpanzees were found, but variation in such patterns was documented for the first time. In the overall sequence, polymorphisms between the canine and the group (M_2 P_4 P_3) reached significant levels. This is due to the relative delay in canine crown formation compared to other teeth. Differences in the basic sequence between males and females were recorded, but are due to minor shifts in the percentages of occurrence for polymorphic sequences which are common to both genders. Perhaps our most important findings are that a) different polymorphic sequences occur in tooth calcification and tooth emergence in chimpanzees, and b) developmental relationships among teeth fluctuate throughout tooth calcification. Thus, characterizations of dental developmental patterns based on particular stages of development cannot necessarily be extrapolated to other stages without supporting data.

The developing dentition is a widely used marker of maturity in both living and skeletal populations and, as such, provides an interface for comparison of growth and development patterns among modern and fossil species. Using such data, paleoanthropologists have attempted to define the life histories of fossil hominids (Aiello and Dean, 1990; Anemone et al., 1991; Bromage, 1987; Conroy and Vannier, 1991a,b; Dean, 1989; Mann, 1975; Smith, 1986, 1989a,b, 1991, 1992, 1994; and others). One of the central issues is whether early hominids (especially the australopithecines) demonstrated prolonged periods of growth and maturation similar to those of modern humans, or shorter periods similar to modern apes.

One avenue of research pertinent to this issue is the comparative study of patterns

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of dental development among modern and fossil hominoid and hominid taxa. The term *pattern* refers to sequences of tooth calcification during dental development, or to the "order in which various teeth develop and emerge in relation to one another" (Conroy and Vannier, 1991b:138). This is distinct from the timing or *chronology* (also referred to as schedule or rate) of such events during dental development, and one can not necessarily be inferred from the other (Anemone et al., 1991; Cheverud, 1981; Conroy and Vannier, 1991b; Simpson et al., 1990). Although rate and pattern of development are fundamentally different, their complex interrelationships during the developmental period make discussion of one difficult without some consideration of the other (see Conroy and Vannier, 1991a; Mann, 1988; Simpson et al., 1990; Smith, 1991).

Research comparing dental development patterns among fossil and modern taxa has a long history in paleoanthropology, and has been conducted using a variety of approaches, including tooth emergence (e.g., Broom and Robinson, 1951, 1952; Clark, 1967; Dart, 1925, 1948; Wallace, 1977), tooth crown and root calcification (Bromage and Dean, 1985; Conroy, 1988; Conroy and Vannier, 1987; Mann, 1975; Simpson et al., 1990, 1991, 1992; Smith 1986), and incremental growth markings in tooth enamel and dentin (e.g., Aiello and Dean, 1990; Beynon and Dean, 1988; Beynon and Wood, 1987; Bromage and Dean, 1985; Dean, 1987a,b, 1989; Dean and Wood, 1981; Mann et al., 1990). As a result, patterns of dental development in both "gracile" and "robust" australopithecines have been characterized in several ways, notably a) human like (Dart, 1925; Mann, 1975, 1988; Mann et al., 1987; Wolpoff et al., 1988); b) pongid like (Bromage and Dean, 1985; Conroy, 1988; Conroy and Vannier, 1987, 1988; Smith, 1986, 1987a,b, 1991); and c) demonstrating different patterns from each other, and *also* from modern humans or apes (Broom and Robinson, 1951, 1952; Bromage, 1987; Beynon and Dean, 1988, 1990; Conroy and Vannier, 1991a,b; Dean, 1985, 1986, 1989; Simpson et al., 1990, 1991, 1992; Smith, 1986, 1989b). A final possibility implied by some researchers is that modern human and ape patterns of dental development are so variable that australopithecine patterns cannot be associated with either (Mann et al., 1987, 1990; Mann, 1988; Wolpoff et al., 1988). Obviously, no true consensus has yet emerged from these comparative studies, but there seems to be growing support for the view that australopithecine fossils demonstrate patterns of dental development which are themselves unique when compared to the overall patterns of either modern apes or humans (e.g., Aiello and Dean, 1990; Anemone et al., 1991; Lewin, 1987).

This statement raises a further issue concerning the analysis of "patterns." A review of the literature reveals at least three usages of the term "patterns" in tooth calcification: a) a "pattern" involving groups of teeth which are functionally or developmentally similar in comparison to other such groups, such as anteriors vs. postcanines (Anemone et al., 1991; Anemone and Watts, 1992; Simpson et al., 1990, 1991, 1992); b) an overall "pattern" or sequence among all teeth which relates the typical order for achievement of developmental events, as used commonly to report sequences of tooth emergence (Conroy and Mahoney, 1991; Kuykendall et al., 1992; Nissen and Riesen, 1964; Schultz, 1935; Smith and Garn, 1987); and c) "patterns" of relative development between particular tooth pairs, which are sometimes referred to as "pairwise sequences" (Smith, 1994; Smith and Garn, 1987).

Because of this range in usage, a general statement that a particular fossil specimen (or species) is characterized by, for example, a "human-like pattern" requires clarification which it may not receive. A further consideration which begs attention in the literature is that any of these "types" of patterns within a (living or fossil) species will demonstrate variation throughout development, or among males and females within the population. So far, this variation has not been well documented, particularly for pongids.

Aside from the scant availability of fossil data, perhaps the primary reason that resolution of these patterns continues to be elusive is the paucity of comparative data concerning modern pongid dental development. A number of recent studies have greatly im-

proved our understanding of dental development in various pongid species, regarding both tooth calcification stages (Anemone et al., 1991; Anemone and Watts, 1992; Dean and Wood, 1981; Simpson et al., 1990, 1991, 1992), and microstructural features (Beynon and Wood, 1987; Dean, 1987a,b, 1989; Dean and Wood, 1981; see also Aiello and Dean, 1990; Lewin, 1985, 1987), but the available baseline data have still not been adequate for the comparative studies needed. For example, no large samples of a single species of living pongids of known age (i.e., other than museum collections of dry skulls) have been analyzed. Additionally, no study has attempted to quantify variations in tooth calcification sequences in any pongid species. In particular, sex differences in tooth calcification sequences have never been seriously explored.

The primary aim of this study was to improve previously available data for chimpanzee tooth calcification in terms of sample size and composition, and to quantify intraspecific variations in the pattern of dental development, especially those due to sex differences.

MATERIALS AND METHODS

The study population was a cross-sectional sample composed of 118 captive chimpanzees (58 male, 60 female) housed at the Laboratory for Experimental Medicine and Surgery In Primates (LEMSIP) at New York University (NYU) Medical Center (39 male, 44 female), and the Yerkes Regional Primate Research Center at Emory University, Atlanta (19 males, 16 females). These chimpanzees ranged in age from 1.5 months to 10 years and 9 months at the time of the study. Examinations roughly corresponded to normal periodic health examinations for each individual on a 3–6-month schedule, and not to birthdates. All yearly age groups are represented in the total sample, but there were no females between 10 and 11 years from either facility.

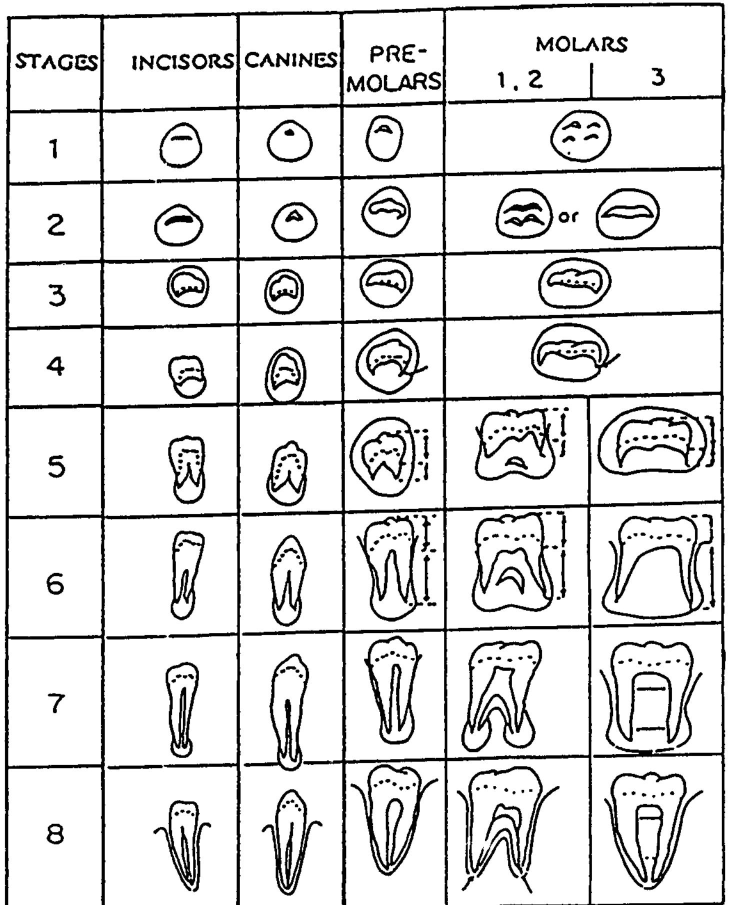
Radiographs were collected using a Min-X-Ray Model P200D Portable Dental X-Ray Unit with nonadjustable power settings of 12 mA at 63 KVP. Collection of radiographs was limited to the left mandibular permanent dentition (I_1–M_3) since reported differences between right and left sides, and between maxilla and mandible, are not statistically significant in humans or chimpanzees (Dean and Wood, 1981; Demirjian, 1979; Nissen and Riesen, 1964). It was also important to minimize the amount of time the chimpanzee subjects were anesthetized.

The aim of the radiographic techniques was to minimize distortion and eliminate overlap from structures on the opposite hemi-mandible, in contrast to results obtained from lateral and anterior full cranial x-rays typically available. Thus, the dental x-ray techniques in this study involved both intraoral (periapical and occlusal) and extraoral (lateral oblique) procedures, as detailed in Frommer (1981). Depending on the age (size) of a given individual, from 3 to 5 radiographs were taken.

Tooth scoring methods are similar to those followed by Demirjian et al. (1973), Demirjian and Levesque (1980), Fleagle and Schaffler (1982), Anemone et al. (1991), and Conroy and Vannier (1991b). An 8-stage system of tooth crown and root calcification was utilized, the stages of which are based on discrete, morphological features of developing teeth, and on relative proportions of crown height and root length (Fig. 1). Although these stages do not represent developmentally equivalent periods or amounts of calcification, this system is preferable to those using criteria such as fractional estimates of crown and root development (Fanning, 1961; Fanning and Brown, 1971; Moorrees et al., 1963; Nolla, 1960), which are accurate only with longitudinal data (i.e., sequential x-rays) (Demirjian, 1986; Garn et al., 1957; Moorrees et al., 1963). Additionally, continuous scales such as those used by Simpson et al. (1990, 1991, 1992) are problematic since tooth calcification does not follow a linear trajectory, but rather its rate varies throughout the developmental period (Anemone and Watts, 1992).

The statistical analysis in this project centers around the documentation of variations in patterns of tooth calcification, also referred to as sequence reversals or polymorphisms (Smith and Garn, 1987). Data for each observation (i.e., each chimpanzee) includes the individual's age at the time of

A



B

Stage	Description
1	In both uniradicular and multiradicular teeth, the initial calcification is visible in the superior region of the tooth crypt as one or a series of inverted cones. There is no fusion of these calcified points.
2	Fusion of the calcified points forms one or several cusps which unite to give a regularly outlined occlusal surface.
3	a) Enamel formation is complete at the occlusal surface. Its extension and convergence towards the cervical region is visible.
	b) Beginning of a dentinal deposit is present below the enamel crown.
	c)The outline of the pulp chamber has a curved shape at the occlusal border.
4	a) Crown formation is complete to the cementoenamel junction.
	b) The superior border of the pulp chamber in uniradicular teeth has a definite curved form, being concave toward the cervical region. If the pulp horns are present, they give an outline like an umbrella top. In molars, the pulp chamber has a trapezoidal form.
	c) Beginning of root formation is observable in the form of a spicule.
5	*Uniradicular teeth:*
	a) The walls of the pulp chamber form straight lines, but may be interrupted by the presence of pulp horns.
	b) Root length is less than crown height.
	Premolars and Molars:
	a) Initial formation of the radicular bifurcation is visible as either a calcified point, or a semilunar mass.
	b) Root length is still less than crown height.
6	*Uniradicular teeth:*
	a) The walls of the pulp chamber approximate an isosceles triangle. The apex ends in a funnel shape.
	b) Root length is equal to or greater than the crown height.
	Molars:
	a) The calcified region of the bifurcation has developed further down from its semilunar stage to give more definition to the roots, which have funnel-shaped endings.
	b) The root length is equal to or greater than the crown height.
7	a) The walls of the root canals are parallel (distal root in molars).
	b) The apical ends of the root canal are open, but NOT funnel-shaped. The periodontal membrane bulges around the root apices.
	c) Proximal and distal roots of multiradicular teeth are parallel--root elongation is complete.
8	a) The apical end of the root canal is completely closed (distal root in molars).
	b) The periodontal membrane has a uniform width around the roots and apices.
	c) In multiradicular teeth, the roots may converge distally.

Fig. 1. The eight stages of tooth calcification used to score dental development **(A)**. Each tooth in each individual was scored independently using the criteria set out in the stage descriptions **(B)** given in this figure (derived from Conroy and Vannier, 1991a,b; Demirjian et al., 1973; Fleagle and Schaffler, 1982).

examination and the recorded stage of development (1–8) for each permanent tooth present. Information about variant sequences is obtained from two-way tabulations between the eight developmental stages for all possible tooth pairs (e.g., I_1–M_1, I_2–M_1, etc.). These tabulations quantify relative developmental sequences between tooth pairs, either at a given stage (e.g., stage 3 in the canine) or during the developmental period as a whole (see Table 1 in the Results). This method is derived from analyses of the sequence of ossification centers of the hand (Garn et al., 1972), of tooth emergence (Smith and Garn, 1987), and of endocranial suture closure (Falk et al., 1989). Initially, the tabulation results were used to determine the "basic" (most commonly occurring) developmental sequence among all teeth. However, the real importance of these tabulations is in the quantification of polymorphisms, i.e., variation from the basic sequence. Separate tabulations were also compiled for males and females in order to examine sex differences in tooth calcification sequence and related polymorphisms.

Sex differences in tooth calcification sequences were examined utilizing Pearson's chi-square test. Further details of these methods are presented in the Results.

RESULTS

The results are organized to examine the three types of patterns described in the introduction, i.e., patterns among groups of teeth, the basic sequence among all tooth types, and sequences between tooth pairs.

Figure 2 presents box plots of the age of achievement of different stages of crown (Fig. 2A) and root (Fig. 2B) calcification for each tooth type in the total study sample of chimpanzees. It is possible to distinguish several groups of teeth from these plots whose patterns can be described as an initial basis for further analysis.

These plots represent the study *population,* and the development of particular individuals cannot be traced. Thus, comments below concerning relationships between particular tooth types are made with respect to the sample ranges and not to individuals.

The first group consists of the incisors, canine, and M_1. Early in development, these teeth achieve developmental stages 1 and 2 approximately concurrently, However, during stage 3, most incisors and canines achieve crown calcification stages relatively late compared to M_1. From crown completion (stage 4) through most of root formation, the M_1 remains the only tooth demonstrating "early" development.

The second group consists of the premolars and M_2 in stages 1 and 2. However, by stage 3, the incisors demonstrate approximately concurrent development with this group. From crown completion on, this group (I_1 I_2 P_3 P_4 M_2) is consistently intermediate in development relative to the M_1 (which is advanced) and the canine and M_3 (which are delayed).

The third group initially includes only the M_3, which clearly begins development later than any other tooth. It is generally the last tooth to achieve any stage of crown or root calcification throughout development, but from stage 3 the canine also demonstrates late development relative to all other teeth. From crown completion (stage 4) on, the canine demonstrates essentially equivalent development relative to M_3.

These patterns of chimpanzee dental development may be summarized as follows:

1. After stage 3, M_1 is advanced relative to development of any other tooth, particularly to either incisor.
2. The premolars and M_2, and the incisors after stage 3, demonstrate approximately congruent development.
3. After initial development with the incisors and M_1, the canine quickly undergoes a relative delay compared to all other teeth but M_3. This is the most significant change in the relative developmental patterns among teeth throughout the development period.

We have identified no major disagreements with previous work with respect to the basic patterns identified above (see Discussion). The aim of the remainder of this analysis is to elucidate the details of these relationships during tooth calcification, and to document variation in these features.

Table 1 presents the percentages of cases

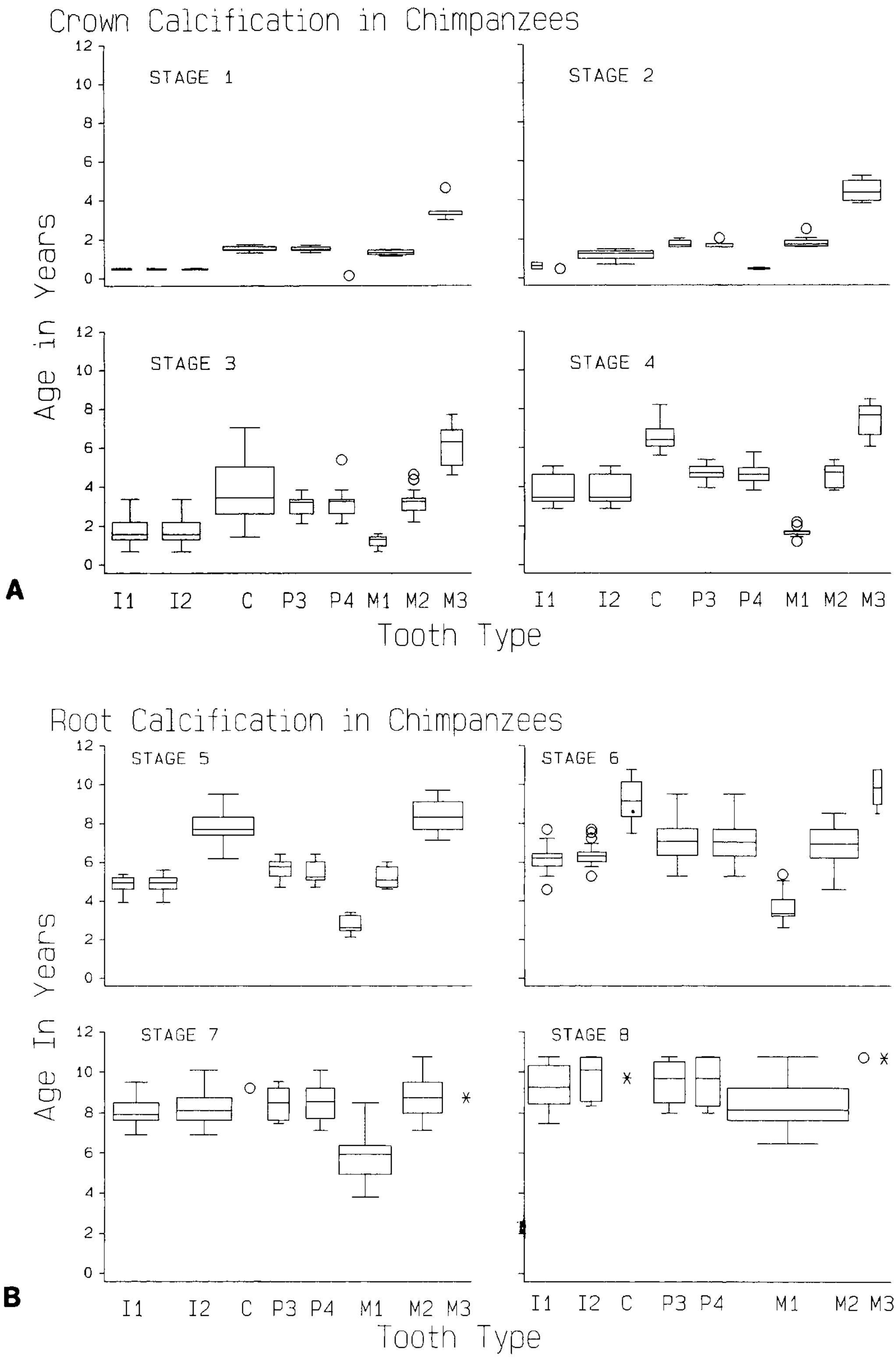


Fig. 2. Box plots of the age of achievement of stages of **A)** crown (stages 1–4) and **B)** root (stages 5–8) calcification. The vertical axis is age in years; the horizontal axis represents the mandibular tooth types I_1–M_3. In the plots for stages 7 and 8 of root calcification, an asterisk (*) indicates that no data were available for the canine and/or M3. The horizontal line across the middle in each plotted box represents the median age (50th percentile); the box outline represents the interquartile range (25th to 75th percentiles); the whiskers extend to the upper and lower adjacent values, defined as values within three-halves the interquartile range; outside values are plotted as individual points.

TABLE 1. Total sample, polymorphisms[1]

	M_1	I_1	I_2	M_2	P_4	P_3	C	M_3
M_1	—	**108** *72*	**109** *77*	**100** *99*	**97** *92*	**95** *90*	**108** *100*	**59** *100*
I_1	0	—	**112** *8*	**99** *54*	**97** *49*	**95** *54*	**108** *81*	**59** *100*
I_2	0	1	—	**100** *47*	**97** *44*	**95** *50*	**109** *82*	**59** *100*
M_2	0	0	*2*	—	**99** *11*	**96** *17*	**98** *65*	**60** *100*
P_4	0	0	*3*	*11*	—	**97** *9*	**95** *67*	**59** *100*
P_3	0	0	*4*	*14*	*6*	—	**93** *67*	**57** *100*
C	0	0	0	*14*	*11*	*12*	—	**58** *57*
M_3	0	0	0	0	0	0	*2*	—

[1] Polymorphisms in growth trajectories of tooth pairs, determined by pairwise tabulation of polymorphic sequences in tooth calcification stages in all tooth pairs throughout chimpanzee tooth development. The sequence of teeth along horizontal and vertical borders is the basic overall sequence of tooth calcification, and was determined by organizing the table with the highest percentages for each tooth pair above the diagonal. In each cell, the numbers in italics represent the percentages of occurrence for each paired sequence shown, and those in bold face represent the number of cases for each pair; these are not repeated below the diagonal. For the sequences above the diagonal, the teeth along the vertical axis achieved a given developmental stage earlier relative to those along the horizontal axis. The cells below the diagonal thus represent the reversals (polymorphisms) from the basic sequence. Corresponding percentages across the diagonal will not sum to 100, since both tooth types in a given pair were scored at the same stage of calcification in a certain number of cases. See comments concerning this table in text.

for pairwise sequences in tooth calcification for the pooled-sex sample of chimpanzees during the entire dental development period, following the method of Smith and Garn (1987) and Smith (1994; see also Falk et al., 1989; Garn et al., 1972). In this matrix, the bottom figures (italics) in the cell for a given pair represent the percentage of cases in which the row tooth was observed in an advanced stage of tooth crown or root calcification relative to the column tooth. Above the diagonal, the top figure (bold face) represents the sample size available for that tooth pair; these are not repeated for corresponding cells below the diagonal. The percentage of cases in which the members of a given tooth pair were found *at the same stage* can be calculated using the sum of percentages in corresponding cells across the diagonal from each other (i.e., I_1 M_1 and M_1 I_1) and subtracting from 1.0.

The order of teeth along the vertical (row teeth) and horizontal (column teeth) axes represents the basic overall sequence for chimpanzee dental development. Above the diagonal, the cells represent data for such "basic sequences." The cells below the diagonal represent data for sequence reversals, or polymorphisms. Smith and Garn (1987) defined polymorphic sequences as variants (reversals) occurring at $\geq$5%, and "significant" polymorphisms as those occurring at $\geq$20%. However, Smith (1994) considered the cutoff for significant polymorphisms at $\geq$15% to be "more convenient" for nonhuman primates, and we also utilize this definition for significance. There are no 'significant' polymorphisms in the total sample, but polymorphisms occurring between 5 and 15% are designated by square brackets enclosing the teeth involved. Thus, the overall developmental sequence in chimpanzees is M_1 I_1 I_2 [M_2 P_4 P_3 C] M_3.

Strictly speaking, Table 1 does not present the type of polymorphism documented by Smith (1994) and Smith and Garn (1987) for tooth emergence, since tooth calcification cannot be recorded as a single event. Although we retain the more simplistic usage of the term "polymorphism" in our discussion, Table 1 actually documents variations in growth trajectories between tooth pairs, i.e., whether or not a particular tooth type (in a population) is typically advanced during its development relative to another. Also, this kind of variation differs from that between growth trajectories of any two individuals. The possible effects of both sources of variation must be taken into consideration when interpreting results from this table.

There are two artificial factors which will affect levels of perceived polymorphism. The first is the sensitivity of the scoring system used. A coarser scoring system such as our 8 stages will detect less variation than a finer one (e.g., estimating the percentage of crown, root, and apical completion). Secondly, all teeth eventually converge to a score of 8 (apical closure) at later stages of maturation. This artificially increases the levels of ties, while suppressing levels for other conditions (non-ties). Thus, we caution against placing undue emphasis on the precise levels of polymorphism documented.

None of the reversals observed in the total chimpanzee sample achieve the 15% level of

TABLE 2. Two-way tabulations of tooth calcification stages between (a) the M_2 and C, and (b) M_2 and P_3, indicating relative developmental relationships (sequences) between these tooth pairs at different stages of tooth development

	a. Canine stage							
M_2 stage	1	2	3	4	5	6	7	8
1		6	1					
2			7					
3			19					
4			7					
5			6	1				
6			7	9	13			
7					7	13	1	
8						1		

	b. P_3 stage							
M_2 stage	1	2	3	4	5	6	7	8
1	4							
2	3	4	1					
3			17	2				
4			1	5				
5				4	3			
6				1	4	24	2	
7						3	9	8
8								1

significance. However, one-rank polymorphisms (i.e., those occupying the first row below the diagonal in Table 1, and occurring at 5 to 15%) are observed for the sequences P_4 M_2, P_3 P_4, and C P_3. Likewise, two-rank polymorphisms occurred for P_3 M_2 and C P_4, and a three-rank reversal was observed for the sequence C M_2.

It is notable that the polymorphisms occurring at the highest percentage levels (approaching 15%) involve the canine, premolars, and M_2. Because of developmental interrelationships among these teeth, their patterns of polymorphism were more closely examined.

Two-way tabulations for tooth development stages between each tooth pair (e.g., I_1–I_2, I_1–C, etc.) show that the polymorphisms among the premolars and M_2 do not follow any systematic trend (see Table 2a and b; only two of these tables are presented due to space limitations). For example, the sequence M_2 P_3 (Table 2b) was documented in some individuals at all stages but (M_2) stages 3 and 8; conversely, the reversal sequence P_3 M_2 was found at all stages but 2, 5, and 6. Similar seemingly random variations between polymorphic sequences for the M_2 P_4 and P_3 P_4 pairs were documented. This is not the case concerning the canine.

In the overall pattern, the canine is generally delayed compared to the premolars and M_2 (see Table 2a), but is polymorphic at levels approaching 15% with each of these teeth as indicated by the sequence (M_2 P_4 P_3 C). However, the two-way tabulations for the canine relative to each of these teeth indicate a complete shift in sequence during stage 3 of crown calcification. Prior to this stage, the canine demonstrates advanced development relative to the premolars and M_2, and is delayed relative to those teeth thereafter. During stage 3, which represents the greatest portion of crown formation, the canine in different individuals may be *either* advanced or delayed relative to the premolars or M_2; the change in sequence occurs during the formation of the large canine crown.

SEX DIFFERENCES

Matrices for tooth development sequences and their polymorphisms are presented separately for males (Table 3a) and females (Table 3b). The overall pattern differs between males and females, and neither males nor females demonstrate the same basic pattern as that for the pooled sample. Additionally, there are no significant polymorphisms when the sexes are analyzed separately, though they exist in the pooled sample. Although samples are small with sexes separated, these points suggest that sex differences are an important aspect of intraspecific variation in the pattern of chimpanzee tooth development.

The polymorphic sequences for males and females are presented in Table 4, including one-, two-, and three-rank reversals and their percentages of occurrence in this sample. The overall sequence for males is M_1 I_1 I_2 P_4 M_2 P_3 C M_3. No significant polymorphisms ($\geq$15%) were documented, but several polymorphisms occurred at lesser percentages (6–13%). The overall sequence for females is M_1 I_1 I_2 M_2 P_3 P_4 C M_3, with two reversals occurring at $\geq$15% (P_3 M_2 and C M_2), and the others occurring at 6–13%.

The major difference between male and female sequences is the shift in position of P_4 relative to M_2 P_3; the rank of various polymorphic sequences among these teeth and with the canine thus differs between sexes.

TABLE 3. Polymorphisms[1]

a. Males

	M_1	I_1	I_2	P_4	M_2	P_3	C	M_3
M_1	—	**51** *71*	**51** *75*	**47** *91*	**47** *98*	**46** *89*	**51** *100*	**31** *100*
I_1	0	—	**54** *7*	**48** *50*	**48** *56*	**47** *60*	**51** *82*	**31** *100*
I_2	0	*2*	—	**48** *44*	**28** *86*	**47** *55*	**51** *84*	**31** *100*
P_4	0	0	0	—	**50** *12*	**48** *10*	**47** *70*	**32** *100*
M_2	0	0	*2*	*10*	—	**48** *15*	**47** *68*	**32** *100*
P_3	0	0	*2*	*6*	*13*	—	**46** *70*	**31** *100*
C	0	0	0	*9*	*9*	*11*	—	**47** *30*
M_3	0	0	0	0	0	0	*2*	—

b. Females

	M_1	I_1	I_2	M_2	P_3	P_4	C	M_3
M_1	—	**57** *74*	**58** *79*	**53** *100*	**49** *90*	**50** *92*	**57** *100*	**28** *100*
I_1	0	—	**58** *9*	**51** *51*	**48** *48*	**49** *49*	**57** *79*	**28** *100*
I_2	0	0	—	**52** *44*	**48** *44*	**58** *38*	**58** *79*	**28** *100*
M_2	0	0	*2*	—	**48** *19*	**49** *12*	**51** *63*	**28** *100*
P_3	0	0	*6*	*15*	—	**49** *8*	**47** *64*	**26** *100*
P_4	0	0	*5*	*10*	*6*	—	**48** *65*	**27** *100*
C	0	0	0	*20*	*13*	*13*	—	**28** *68*
M_3	0	0	0	0	0	0	0	—

[1] Matrices tabulating polymorphic sequences for pairwise tooth calcification stages in all tooth pairs throughout tooth development for (a) males and (b) females. Read as in Table 1.

TABLE 4. Summary of polymorphisms in tooth calcification for males and females[1]

	Males		Females	
Rank	Polymorphism	Percent	Polymorphism	Percent
One-rank	C P_3	11	C P_4	13
	P_3 M_2	13	P_3 P_4	6
	M_2 P_4	10	P_3 M_2	15
Two-rank	C M_2	9	C P_3	13
	P_3 P_4	6	P_4 M_2	10
			P_3 I_2	6
Three-rank	C P_4	9	C M_2*	20
			P_4 I_2	5

[1] Each sequence represents a reversal from the basic sequence for males or females, and a particular polymorphism may occur at different ranks in each sex. Significant polymorphisms (occurring at ≥ 20%) are indicated by an asterisk (*).

For example, C P_4 is a one-rank polymorphism in females, and a three-rank reversal in males. These sequence shifts are all the result of rather small differences in percentages—most are between 2 and 4%.

For example, two reversals were observed only in females at levels which are defined as polymorphic. Reversals between the premolars and I_2 are observed at 5% (P_3 I_2) and 6% (P_4 I_2) in females. However, the sequences P_3 I_2 and M_2 I_2 were recorded in males, but only at trace levels of approximately 2% (involving one individual)—thus they are not polymorphic by definition.

All of the polymorphisms involving the I_2 occur only during stages of root formation, etiher at I_2 stage 5 or stage 7. This indicates that the I_2 in some individuals is slightly delayed in root formation compared to the premolars or M_2, which may be related to differences in root length, or in rates of root formation (Dean and Wood, 1981) between anterior and posterior teeth.

Pearson's chi-square test was utilized in order to determine whether any of the sex differences found are statistically significant. The graphic plots as well as the results in Table 1 suggest that there is increased variability, and therefore a greater chance of polymorphisms, for some teeth at certain stages (e.g., the canine at stage 3 of crown formation). Thus, the Chi-square test was utilized in order to examine such questions as, "Is the developmental status of M_2 (i.e., the particular stages in which the M_2 is found) significantly different in males vs. females when the canine is in stage 3?" For each of the eight tooth types, this requires a comparison with each of the remaining seven teeth on eight stages, thus a total of 448 tests. Of this total, only 286 had sufficient data (i.e., no zeros) to run, and only 83 of these had sufficient cell totals ($n > 5$) to produce reliable results. After all this, only five results came up with significant Chi-square values ($P \leq 0.05$). These follow no biologically meaningful pattern and may be viewed as being due to random effects (Type II errors).

A second Chi-square test was constructed in the following manner. It was determined that the overall sequence in both males and females differed from that for the pooled

sample, and that the same polymorphic sequences were generally present in both sexes, but at varying frequencies. These polymorphisms involve the canine, premolars, and M_2. Thus, it is possible to ask the question, "Do males and females demonstrate significant departures from the pooled sequence [M_2 P_4 P_3 C]?" The tests were set up to determine whether the number of males exhibiting the polymorphism for a particular pooled sequence (e.g., M_2 P_4) differed significantly from the females demonstrating the same polymorphism. None of these Chi-square results achieved levels of statistically significant differences at $P \leq 0.05$.

DISCUSSION

This analysis constitutes an examination of patterns of tooth calcification in the chimpanzee at several levels of resolution: developmental relationships among different tooth types, the overall sequence of calcification among all tooth types, and pairwise sequences and their reversals. The most important contributions of this study concern the quantification of polymorphic sequences, and the analysis of sex differences in patterns of dental development.

This study was initially conducted in order to improve comparative baseline data for the analysis of fossil hominid dental development patterns. The ongoing controversy revolves, most generally, around the question of whether the patterns of dental development (including both tooth emergence and calcification) recorded in fossils of early hominids most resemble aspects of modern human, or of modern ape, dental development. We summarized the basic tooth development patterns in our sample of chimpanzees in terms of relative developmental relationships between a) M1 and I1, b) M2 and the premolars, and c) the canine and all other teeth.

These features are essentially the same as those discussed in earlier studies comparing tooth development (including both tooth emergence and calcification) in apes, humans, and fossil hominids (Aiello and Dean, 1990; Anemone et al., 1991; Anemone and Watts, 1992; Clements and Zuckerman, 1953; Conroy, 1988; Conroy and Mahoney, 1991; Conroy and Vannier, 1987, 1988, 1991a,b; Dean, 1985, 1987b; Dean and Wood, 1981; Garn et al., 1957; Kraemer et al., 1983; Krogman, 1930; Kuykendall et al., 1992; Mann, 1975, 1988; Mann et al., 1987, 1990; Nissen and Riesen, 1964; Schultz, 1935; Simpson et al., 1990, 1991, 1992; Smith, 1986, 1987a,b, 1989a, 1994; and others), although they have previously been defined in terms of I1 development relative to M1 emergence, relative development of the M2 versus the premolars and canine, and general delay of the canine and M3 (the jaw in question is not always indicated).

With our quantitative results in hand, it is now possible to discuss variation in patterns of chimpanzee dental development such as those just mentioned. Unfortunately, direct and detailed comparisons with dental developmental patterns in humans and other nonhuman hominoids will remain inconclusive until quantitative analyses of tooth calcification sequences in other species are presented expressly for this purpose. In the meantime, we can provide some useful clarification of relevant features of chimpanzee tooth calcification patterns.

There are several studies of the developing chimpanzee (or pongid) dentition available in the literature, including those of tooth emergence (Clements and Zuckerman, 1953; Conroy and Mahoney, 1991; Kraemer et al., 1983; Krogman, 1930; Kuykendall et al., 1992; Nissen and Riesen, 1964; Schultz, 1935), age standards for tooth calcification (Anemone et al., 1991; Dean and Wood, 1981), and analyses of relative developmental relationships among teeth (Anemone and Watts, 1992; Simpson et al., 1990, 1991, 1992). However, the only source located in the literature which quantifies polymorphic sequences of tooth development in chimpanzees (in this case, of tooth emergence) is Smith (1994). We make detailed comparisons with Smith's results in order to identify the differences between tooth emergence and tooth calcification sequences, and to more completely describe aspects of variation in tooth development in chimpanzees; information from other studies will be incorporated where relevant. It is also relevant to note that this study includes chimpanzees which made up part of Smith's chimpanzee

sample (i.e., most of those from Kuykendall et al., 1992).

The overall sequences from Smith (1994) for mandibular tooth emergence in a pooled sample (males and females) of chimpanzees is M_1 I_1 I_2 [M_2 P_4 = P_3] C ([ ] indicate 'significant' polymorphisms at ≥15%, and = signifies polymorphisms greater than 40%; Smith did not include the M_3). Dean and Wood (1981) provide partial sequences for chimpanzees in their Table 1 from which the following reconstructed sequence, including all mandibular teeth but the canine, can be derived (the equal signs indicate teeth which were always found in the same stage): M_1 I_1 = I_2 P_3 = P_4 = M_2 M_3. Our pooled sequence for mandibular tooth calcification in chimpanzees is: M_1 I_1 I_2 (M_2 P_4 P_3 C) M_3 (parentheses indicate polymorphic levels between 5 and 15%; our data do not include the maxilla). Thus, allowing for variability, the basic sequence appears to be very similar for tooth emergence and tooth calcification in the chimpanzee samples studied. The main differences between studies involve the polymorphisms for the premolars and the canine. Our sequences for males and females separately both differed from the pooled sequence as described in the Results, but these cannot be compared to other studies.

Smith (1994) identified the following polymorphic sequences in tooth *emergence* which "clearly separate chimpanzees from humans," i.e., that are characteristic of chimpanzees: a) polymorphisms involving the premolars or M2 versus I2 (e.g., P3 I2), which were found at "substantial levels" (up to 28% in the maxilla) in chimpanzees, but were rare or absent in humans; b) polymorphisms involving the canine, which are totally absent in chimpanzees, but occur at high levels for some variants in human tooth emergence (e.g., 27% for P_3 C in the mandible); and c) the mandibular I_1 M_1 emergence sequence, which is again absent in chimpanzees, but occurred at 36–52% in Smith's human sample (Smith and Garn, 1987), depending on the gender and population group in question.

In our data, polymorphisms for tooth *calcification* involving I_2 and the premolars or M_2 occur only at trace levels (<5%) in the pooled sample (males and females) of chimpanzees (Table 1). As noted, however, the P_3 I_2 and P_4 I_2 sequences do occur in female chimpanzees at levels which are defined as polymorphic (5–6%) (Table 3b). Smith (1994) reported much higher levels for these variants for tooth emergence in the maxillary dentition for chimpanzees, but those for the mandible were between 3 and 6% for the P_3 and P_4; i.e., the premolar polymorphisms occur at roughly similar levels for mandibular tooth emergence *and* calcification. However, the M_2 I_2 polymorphism occurs only at trace levels for tooth calcification (our data), and at relatively high levels (13% in the mandible and 28% in the maxilla) for tooth emergence (Smith's data).

This difference between M_2 I_2 polymorphism levels in tooth emergence and tooth calcification does not appear to be explainable as a general phenomenon in tooth calcification (i.e., that polymorphisms in calcification sequence are less common than those in emergence sequences), since notable differences were not observed for other tooth pairs. It is possible that there is a methodological effect on the calculated levels of polymorphisms in our analysis due either to a) discrepancies in scoring a continuous process (tooth calcification) verses a single event (tooth emergence), or b) to the inclusion of data for developmental "ties" between tooth pairs in our analysis (as discussed in Materials and Methods). However, in either case, we would expect consistent differences among all tooth pairs in the matrices, and not in only a single case. Thus, if these effects are present, they do not fully explain the particular difference in polymorphism levels for M_2 I_2 between tooth emergence and tooth calcification.

There is no a priori reason to expect that high levels of polymorphism in tooth emergence should be associated with the same in tooth calcification for a given tooth pair. Studies by Shumaker and El Hadary (1960), Grøn (1962), and Fanning (1961) have demonstrated that the amount of root formed at tooth emergence varies amongst tooth types, and that rates of tooth calcification and tooth emergence are independent. In other words, tooth eruption does not correspond to a given amount of root elongation or tooth calcification (Shumaker and El Hadary, 1960). Fur-

thermore, Garn and Lewis (1957) have shown that sequences of tooth calcification and emergence change as the tooth moves toward occlusion. Thus, the difference in polymorphism levels is probably best explained in terms of variability in tooth calcification status at tooth emergence. At any rate, those tooth emergence polymorphisms which Smith (1994) identified as distinctively chimpanzee do *not* occur at significant *levels* in our analysis of chimpanzee tooth calcification.

The relative position of the canine has been identified as a major difference between ape and human tooth emergence sequences (Clements and Zuckerman, 1953; Swindler, 1985). Similarly, the canine is "the single tooth with the most contribution to [emergence] sequence polymorphism" in humans, while tooth emergence polymorphisms involving the canine are totally lacking in chimpanzees (Smith 1994, p. 68). In contrast, the only polymorphisms in our chimpanzee tooth calcification data which approach the significance level of 15% are those involving the canine and premolars or M_2. Reversals of this type remain relatively high (though not at significant levels) in both male and female chimpanzees, although they are higher in females (13–20% vs. 9–11% in males).

The occurrence of these polymorphisms in tooth calcification sequences in the absence of such for tooth emergence sequences can be related to the lengthy time requirement for canine crown development. Canine crown formation takes roughly 6 years in chimpanzees, while the premolar and M2 crowns each develop in about 2.5 to 3 years (Kuykendall, 1996). In relative developmental terms, initial calcification of the chimpanzee canine crown is advanced relative to that for the premolars and M2, but canine development becomes progressively delayed during crown calcification (stage 3). Thus, the polymorphisms recorded for tooth calcification represent this developmental shift in the canine's relative position, which is completed by the time the tooth emerges.

It is possible that canine polymorphisms in humans occur during both tooth emergence and calcification, but they would not be due to a shift in sequence since the human canine does not undergo the delay seen in chimpanzees. Thus, the value of canine sequence polymorphisms for discriminating between chimpanzees and humans is presently unknown. It may be that the particular teeth involved, or the frequencies at which canine polymorphisms occur are characteristically different in the two species, as reported in Smith (1994) for some tooth pairs.

Finally, it is interesting to note that the canine in at least some fossil hominid specimens demonstrates delayed development (Conroy and Vannier, 1987; Wallace, 1977), despite the fact that its crown is reduced in size compared to modern apes (i.e., more similar to human canines). Thus, although canine tooth emergence patterns in apes and humans are clearly distinctive (as is canine morphology), tooth calcification patterns for the canine may prove to be confusing rather than illuminating (e.g., see Anemone and Watts, 1992; Simpson et al., 1990).

The M1–I1 sequence has received much attention in the literature concerning ape, human, and fossil hominid patterns of tooth development, and is probably the most widely hailed, though still controversial, criterion in use for distinguishing "ape" from "human" dental development patterns (Bromage, 1987; Broom and Robinson, 1951, 1952; Clements and Zuckerman, 1953; Conroy and Vannier, 1987, 1988, 1991a,b; Dean, 1985; Mann, 1975, 1988; Mann et al., 1990; Schultz, 1935; Wallace, 1977; Wolpoff et al., 1988).

For tooth emergence, the reversal sequence I_1 M_1 occurs at levels between 36 and 52% (vs. 6–13% for the maxilla) in humans (Smith and Garn, 1987; Smith, 1994), and is totally lacking in chimpanzee tooth emergence sequences (Smith, 1994; also Conroy and Mahoney, 1991; Kuykendall et al., 1992; Schultz, 1940). Furthermore, the present data document that this sequence polymorphism does not occur at *any* stage of tooth calcification in chimpanzees. In fact, the M_1 may be advanced relative to I_1 by as much as three stages after (M_1) crown completion. Thus, the lack of I_1 M_1 sequences in chimpanzees appears to be a consistent and highly useful distinguishing characteristic for this species.

However, there is still a possibility for con-

fusion of human and chimpanzee M_1 I_1 patterns. The chimpanzee M_1 and I_1 are found at the *same* developmental stage in 28% of the recorded cases (see Table 1). Eighty percent of these cases occur at stage 3 of (M_1) crown formation or stage 8, i.e., root completion. The M_1 and I_1 demonstrate equivalent stages of development in chimpanzees only at these two predictable periods of M_1 calcification. Stage 3 is a developmental period of long duration, thus the incisor has a chance to "catch up" to the molar tooth. Stage 8 is the final stage, after which no further development occurs; thus, a similar "catch up" event occurs.

Thus, it may be that changing developmental relationships among teeth may confound attempts to make interspecific distinctions *at some, but not all, stages of tooth calcification.* This is an important consideration in light of controversies involving "ape-like" patterns in modern humans (e.g., Conroy and Vannier, 1988; Mann, 1988; Wolpoff et al., 1988).

SEX DIFFERENCES

Our data demonstrate that there exist differences in the pattern of tooth calcification between male and female chimpanzees, and in the percentage-levels of the polymorphisms present. These two results are interrelated; the sex differences in overall sequence are the source of the differing polymorphism levels. The sequence differences involve only the premolars and M2, but these are precisely the teeth which are involved in significant polymorphisms with the canine in the pooled sample (polymorphic variation is higher in the pooled sample than in either sex separately). This does not imply that male and female chimpanzees can be fully distinguised on these differences alone; the same polymorphic sequences are found in both sexes, but at differing percentages. The contribution of these differences to intraspecific variation must be acknowledged in order to attain a thorough understanding of growth and development in this species. Sexual dimorphism does have developmental consequences in chimpanzees.

For example, the occurrence of polymorphisms for the canine relative to the P_3 P_4 M_2 group differs between the sexes. Although the canine is usually delayed compared to any of the three teeth in both sexes, it is not involved in any significant polymorphisms in males. In females, the three-rank polymorphism C M_2 occurs in about 20% of cases. This reversal occurs in only 9% of cases in males, and is only a two-rank polymorphism. In other words, the canine appears to be "more delayed" in males relative to the premolars and M_2. This is supported by the fact that calcification of the male chimpanzee canine crown requires approximately one year longer for completion compared to females, while such sex differences are not found for other teeth (Kuykendall, 1996).

In summary, it seems that the premolar–M_2 sequence differences are related to the developmental relationships between these teeth and the canine, as well as to their own interrelationships (see Garn and Smith 1980).

A more subtle corollary of our results concerns those teeth which do *not* demonstrate sex differences, i.e., which are less variable. These teeth appear to follow very consistent patterns which may be more useful for determining "chimpanzee" features of dental development. In particular, these include the M1 and the incisors, but sequences among the canine and incisors, and the canine and M3 may also be relevant. As Smith (1994) has pointed out, the best discriminators are those sequences which appear at percentages approaching 100 in one species, and approaching 0 in another. Obviously, the true value for interspecific discrimination of any tooth calcification sequences in chimpanzees can only be determined once adequate analyses of human data are made available.

Finally, there remains the issue of statistical testing for sex differences. None of the sex differences observed were found to obtain statistical significance following a systematic pattern. However, the tests utilized were aimed at determining whether the different levels of polymorphism were statistically significant between the sexes. Perhaps the more pertinent issue is that the shift in the overall pattern had a consequent effect on the location and rank for particular polymor-

phisms, regardless of whether they occurred at dramatically different percentages between males and females (the differences were in fact, very small). In other words, the fact that male and female chimpanzees are characterized by differing sequences (basic and polymorphic) is in and of itself a biologically significant result, and indicative of the complexity of these growth processes.

CONCLUSIONS

Our results generally support previous characterizations of tooth calcification patterns in chimpanzees, particularly those concerning relationships between I_1 and M_1, the premolars and M_2, and the canine and all other teeth. Rather than reiterating the specific results discussed above, we would like to emphasize the following general conclusions which are probably relevant to any analysis of tooth calcification patterns in chimpanzees, humans, or fossil hominids:

1. Tooth calcification and tooth emergence polymorphisms are to some degree independent; sequences which are not found for tooth emergence may occur at significant levels for tooth calcification in the same species, or vice versa. These differences are explainable in terms of the inconsistent relationship between tooth calcification status and tooth emergence.
2. Interspecific distinctions based on tooth development patterns must consider the stage(s) of development at which comparisons are made, since developmental relationships between and among teeth fluctuate throughout tooth calcification. Generalized characterizations of developmental relationships based on particular stages of development are not necessarily valid throughout development, particularly without adequate data for all species compared. This also certainly affects comparisons between studies utilizing different systems for scoring tooth development.
3. Sex differences in chimpanzee tooth calcification sequence consist of minor shifts in levels of different polymorphisms which are found in both sexes, and probably relate to differences in the timing of calcification periods between males and females. Although no differences were found to exist at levels of statistical significance, their presence does have significance for the analysis of complex biological processes.

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